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ON THE PHYLOGENETIC RELATIONSHIPS OF THE GIANT PANDA (*AILUROPODA*) TO OTHER ARCTOID CARNIVORA

By William K. Gregory

INTRODUCTION

In 1875 Milne-Edwards in a memoir on *Ailuropoda melanoleuca* published the conclusion that this curious beast must occupy a position intermediate between the bears and the panda (*Ailurus fulgens*). In 1891 Flower and Lydekker in their work on 'Mammals, Living and Extinct' placed "*Aeluropus*" in the Ursidae, and it is indeed so bear-like in general appearance that it has often been called "the parti-colored bear." In 1895 Winge (as interpreted by Bardenfleth, 1914), "places still more exclusively *Aeluropus* among the Ursidae as a very near relative of the *Hyaenarctus*, these two forming together a branch of the Ursine stem, whereas *Aelurus* belongs to the Procyonine stem of Procyonidae whose root is *Bassaris*. A true relationship between the two species is thus out of the question." In 1901, however, Lankester, assisted by Lydekker, reanalyzed the evidence from external characters, dentition, skull, limbs and feet, and came to the conclusion that "*Aeluropus*" is a member of the Procyonidae, or raccoon family. They also divided that family into two subfamilies: (a) Procyoninae, containing the American genera *Procyon*, *Nasua*, and (b) Aelurinae, containing the Asiatic genera "*Aelurus*" and "*Aeluropus*":

In 1914 Bardenfleth, after an extended comparative analysis of the dental and osteological characters of *Ailuropus*, concluded that its resemblances to *Ailurus* were due to a convergent development of the molar teeth based on herbivorous diet and that its closest affinities were with the ursids of the *Hyaenarctos* group. In 1915 A. S. Woodward described a well-preserved skull of a giant panda, closely related to *Aeluropoda melanoleuca*, from a cave at Magok, Upper Burma, giving it the name *Aelureidopus baconi* and expressing the following opinion as to the relationships of "*Aeluropus*":

"It is so completely intermediate between the Procyonidae and the Ursidae, that it is sometimes placed in the one family, sometimes in the other; and its relationships to the Pliocene *Hyaenarctos* are so obvious, that it must doubtless be regarded as a somewhat modified survivor of

the common stock from which the Procyonidae and Ursidae have diverged. No closely related fossil forms, however, have hitherto been recorded; and the recent discovery of a skull of an allied extinct species is therefore of interest."

In 1923 Matthew and Granger, in describing the type of *Aeluropus fovealis* from the Pliocene of Szechuan, China, said: "The affinities of

Fig. 1. *Ailurus fulgens.* Side view of skull. × 1.

Aeluropus appear to be with *Hyaenarctos,* as has been observed by Lydekker, Winge and other writers. Its systematic position appears to be clearly in the family Ursidae, although of a distinct subfamily from the true bears. Bardenfleth has presented the evidence for this view very clearly."

In 1932 in a valuable article on 'The Pandas or Cat-bears' Sowerby again directed attention to the many close resemblances between the giant panda and the little panda and concluded that "it would be more in keeping with the genetic facts of the case if the giant and little panda were placed together in a family by themselves, to which the name

Aeluridae might be given." On the other hand, Boule and Piveteau in their great work 'Les Fossiles' (1935, p. 778) refer *Aeluropus* to the Ursidae, placing it between *Indarctos* of the Siwaliks and *Arctotherium* of the Pliocene and Pleistocene of North and South America.

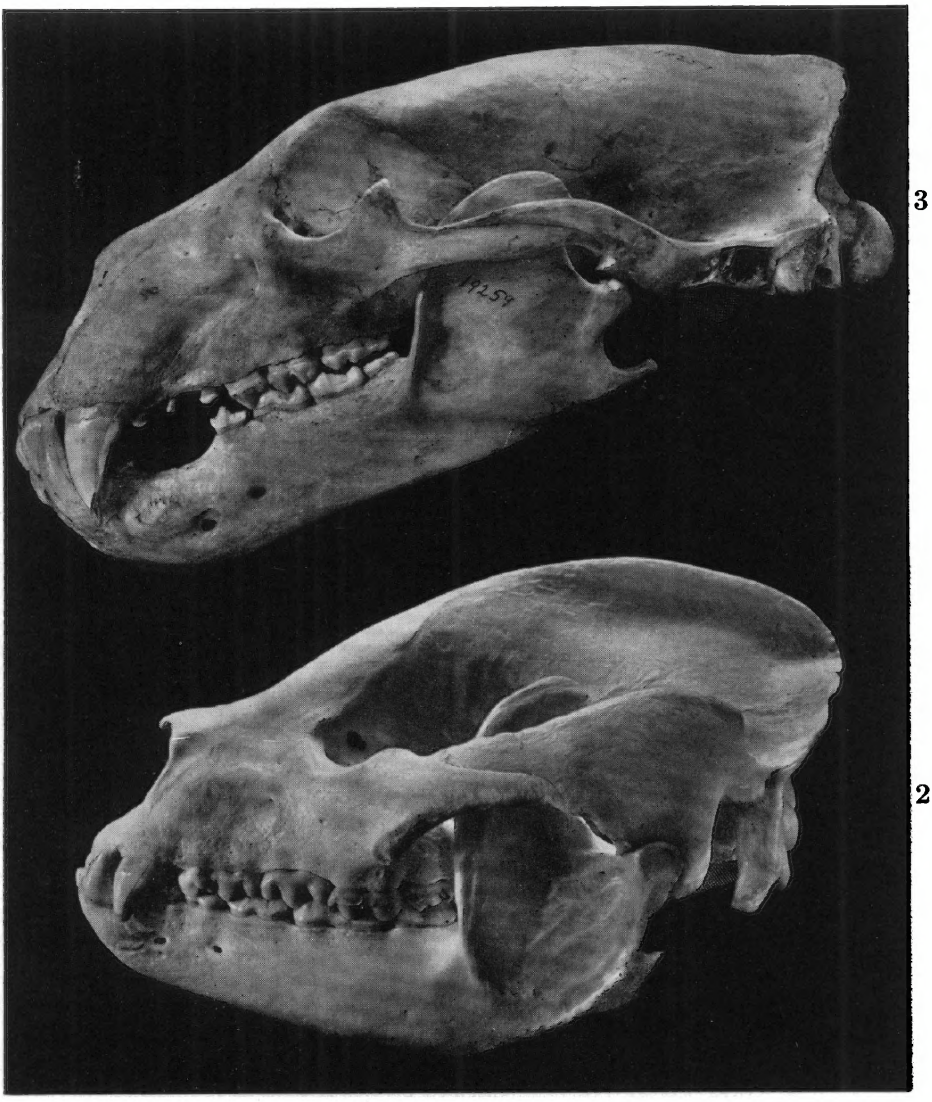

Fig. 2. *Ailuropoda melanoleuca.* Side view of skull. × *circa* 1/3.
Fig. 3. *Thalarctos maritimus.* Side view of skull. × 1/3.

Thus, from the time of its discovery down to the present day the giant panda has been classified by most authors as a peculiar branch of the bears related to *Hyaenarctos*, but several authors have regarded it as a sort of intermediate between the bears and *Ailurus*, while Lankester and Lydekker held that it belongs with *Ailurus* as a subfamily of the Procyonidae but is related more remotely to *Hyaenarctos* and the Ursidae and still more remotely to *Canis*.

The preservation of the principal viscera of *Ailuropoda* by Mr. Donald Carter of the Dean Sage West China Expedition has made it possible for Mr. H. C. Raven to make comparisons with the viscera of other carnivores and has led him to conclude that Lankester and Lydekker were essentially correct in referring this genus to the Ailurinae. However, in view of the opposing judgments of other authors, it appeared desirable to make a new and independent analysis of the characters of the dentition and skull of *Ailuropoda* in comparison with those of fossil and recent canids, procyonids (including *Ailurus*), hemicyons and modernized bears. Through the kindness of Dr. H. E. Anthony, Curator of Mammals in this Museum, I have been privileged to study the several skulls of *Ailuropoda melanoleuca* secured by the Dean Sage West China Expedition, while Dr. Walter Granger has placed at my disposal an incomplete skull and nearly complete mandible of *Aeluropus fovealis*, together with a number of isolated teeth.

COMPARISON OF THE CHEEK TEETH OF *AILUROPODA* WITH THOSE OF THE *HEMICYONS* AND THE BEARS

After repeatedly studying and handling much fossil and recent material bearing on the problem in hand, I feel that it is no longer necessary to question the soundness of the late Dr. W. D. Matthew's general conclusions concerning the evolution and relationships of the main divisions of the order Carnivora. In his great memoir on the Carnivora and Insectivora of the Bridger Basin, as well as in other papers, Matthew showed that the Eocene family Miacidae was the parent family of all the modern dogs, bears, raccoons, civets, hyenas, cats, etc. In contrast with the typical creodonts, these Miacidae always had the chief cutting blades developed on the fourth upper premolar and the first lower premolar, which teeth are therefore called "the carnassials." The most primitive genera of the family had the carnassials quite large and highly cutting in character, much like those of a dog, but in several specialized derivatives of the family the shearing blade of the upper carnassial became reduced and the tooth showed a tendency to develop low conical

cusps. My studies (unpublished) on recent and fossil Canidae, Procyonidae, Ursidae, Mustelidae, Viverridae, etc., have also convinced me that Matthew was again right in regarding the following two divergent conditions as being entirely secondary: (a) the progressive enlargement and complication of p^4 and m_1, culminating in the excessively shearing teeth of *Cryptoprocta*, the hyenas and the cats; (b) the degeneration and reduction of these teeth, in the bears, as well as in the Procyonidae. These divergent processes occur independently in different families.

The experience of palaeontologists suggests that when the systematic position of a mammal is in doubt a study of the patterns of the premolar crowns may yield points of high diagnostic value with regard to family relationships. We may therefore begin by comparing the premolars of *Ailuropoda* with those of the most primitive known representative of the bear series; this is the Pliocene *Hemicyon*, the dentition of which has been well described by Childs Frick (1926).

The second and third upper premolars of *Ailuropoda* (Fig. 4) are large and richly cuspidate teeth, whereas in *Hemicyon* and the bears the corresponding teeth are small, weak and degenerate. The upper "carnassial" (p^4) of *Ailuropoda* is a very large complex tooth with three large cusps on its outer wall, a small antero-internal cusp and a very large postero-internal cusp; in *Hemicyon*, on the contrary, p^4 retains much more of its primitive carnassial appearance, having a pronounced posterior blade, no parastyle cusp and only a small single internal cusp.

Similarly all the lower premolars of *Ailuropoda* (Fig. 9) are large and highly progressive teeth, while those of *Hemicyon* are small and somewhat degenerate as compared with those of the primitive Canidae. The lower carnassial (m_1) of *Ailuropoda*, although disguised by secondary cusps, retains traces of its former carnassial function. It has, however, become much widened transversely, especially across the talonid. In *Hemicyon*, on the contrary, the lower carnassial (m_1) retains most of its primitive dog-like character and is indeed anteroposteriorly elongate and compressed.

In brief, *Ailuropoda* is very widely separated from *Hemicyon* by its far more complex p^2, p^3, p^4, and p_2, p_3, p_4, m_1. If we now compare *Hemicyon* with the bears, we see that its upper and lower premolars and m_1 appear to afford an almost ideal starting-point for the more or less degenerate and specialized condition of these teeth in the bears. The main difference between *Hemicyon* and the typical bears is that in the former p^4 is less reduced than in the late Tertiary and Pleistocene bears, where its small size is a character wholly foreign to all primitive Eocene

Miacidae and a relatively recent specialization not older than the initial anteroposterior elongation of m^1, m^2.

P^4 of *Ailuropoda* agrees with that of *Hyaenarctos* in having a parastyle, but differs in having two large internal cusps instead of one. It is true that Winge (1895–96) and Bardenfleth (1914) tried to show by examination of the position of the roots that the inner cusps of the carnassial of *Ailuropoda* were homologous with those of *Ursus* and *Hyaen-*

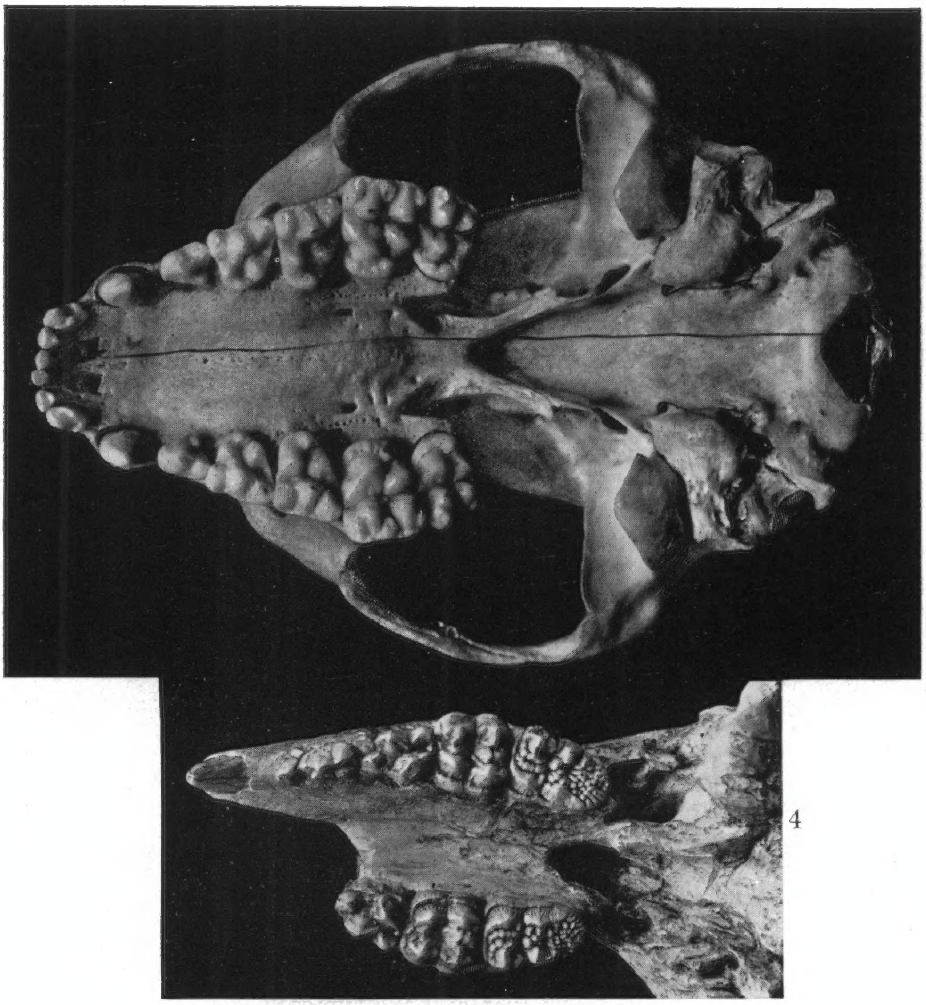

Fig. 4. *Ailuropoda fovealis.* (?) Upper Pliocene, China. P^2–m^2. × 1/3.
Fig. 5. *Ailurus fulgens.* Under side of skull. × 1.

arctos, not with those of *Ailurus*. According to this view the antero-internal cusp of p^4 in *Ailuropoda* represents a new upgrowth from the cingulum, while the larger obliquely placed cusp represents the backwardly displaced main internal cusp of the carnassial of the bears. But

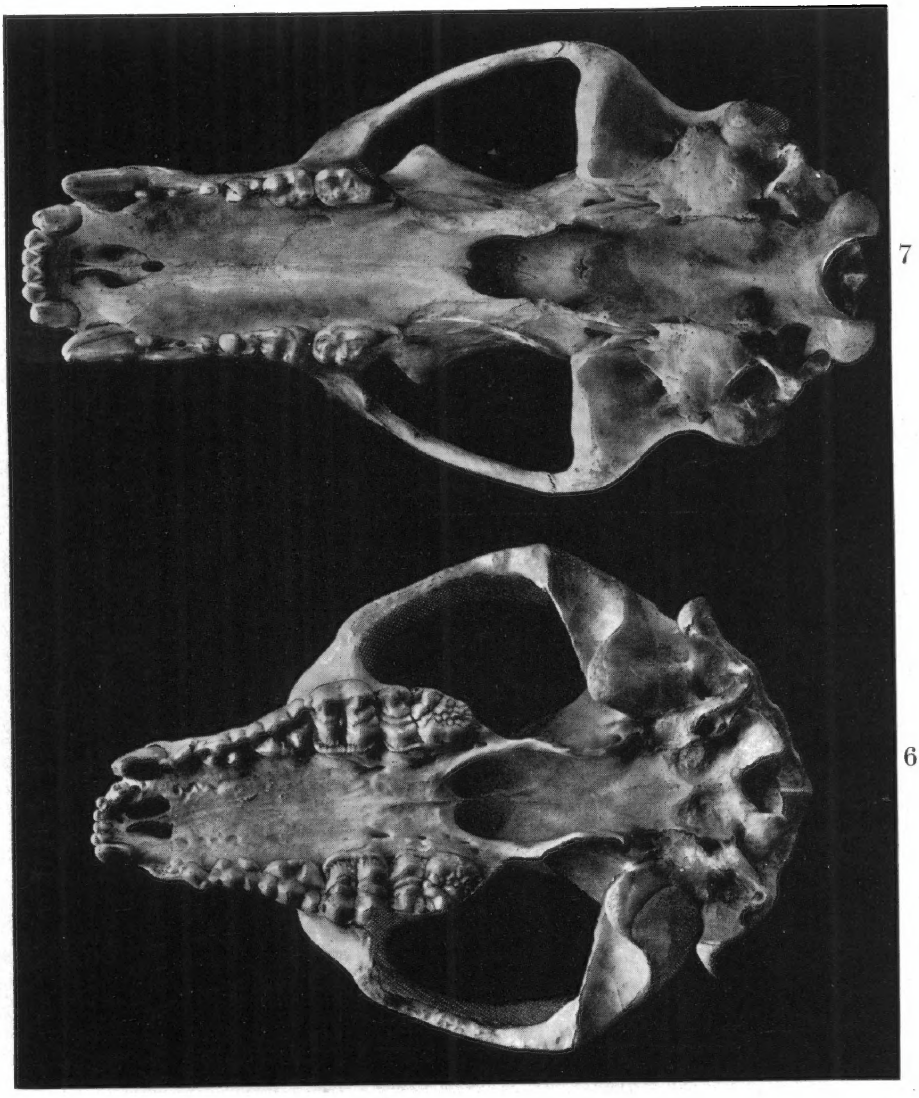

Fig. 6. *Ailuropoda melanoleuca*. Under side of skull. × 1/3.
Fig. 7. *Thalarctos maritimus*. Under side of skull. × 1/3.

after a careful review of the facts I conclude, on the contrary, that the postero-internal cusp of p^4 of *Ailuropoda* is fully homologous with the corresponding cusp in *Ailurus* and *Parailurus*, but not at all homologous with the sole internal cusp of *Hyaenarctos* and the bears, which is progressively displaced backward. These differences alone would be insufficient to exclude *Ailuropoda* from descent from *Hyaenarctos*, but taken in connection with many other points they serve to emphasize the conclusion that the ancestry of *Ailuropoda* must be sought elsewhere than in *Hyaenarctos*, which is assuredly related on the one hand to *Hemicyon* and on the other to the ancestors of the short-faced bears, with which it is connected by the genera *Indarctos* and *Ursavus*.[1]

The upper molars (m^1, m^2) of *Ailuropoda* (Figs. 4, 6) are remarkable for their relatively immense size and for the rich development of "secondary polyisomeres" in the form of small accessory tubercles on the surface of their crowns. In these features they are far more specialized than m^1 and m^2 of *Hemicyon*, which are much nearer to the primitive dog-like condition. At first sight the upper molars of *Ailuropoda* do indeed suggest those of typical bears, but they are much wider, more tuberculated and less elongated anteroposteriorly. The first upper molar of *Ailuropoda* differs from those of *Hyaenarctos*, *Lydekkerion* and *Indarctos*, which are well figured by Frick (1926), in its greater width, rich tuberculation, very large proto- and meta-conules and enlarged internal cingulum. In the three last-named genera the first upper molar seems to be approaching that of the Malayan bear (*Helarctos malayanus*).

Both m^1 and m^2 of *Ailuropoda* differ from those of the short-faced extinct bears (*Arctotherium*) in important characters: they are decidedly wider transversely and shorter anteroposteriorly, their para- and metacones are on the extreme outer border of the crowns instead of being further in toward the middle of the tooth, their internal cingulum is massive and crenulated instead of being nearly vestigial.

The second upper molar (m^2) of *Ailuropoda* is much less elongate than that of the typical bears, but more elongate than that of either *Hyaenarctos* or *Indarctos;* it is distinguished from the corresponding tooth in all the bears, however, by the presence of a double row of vigorously developed cuspules between the inner surface of the reduced paracone and the metacone, as well as by the presence of a large "meta-

[1] Childs Frick, whose excellent work on the Hemicyoninae (1926) supplies abundant evidence of the intermediate position of these genera between dogs and bears, yet prefers the idea that the lines represented by *Canis*, *Amphicyon*, *Procyon* and *Ursus* all run back quite independently to the Oligocene. This is partly because he seems not to have realized that the premolars of bears are reduced and degenerate, just as the enlargement of their upper molars is secondary, and that, as Matthew maintained, the large carnassials and small molars of the earliest dogs and miacids represent the primitive condition for all Arctoidea.

Fig. 8. *Ailurus fulgens.* Lower jaw. × 1.
Fig. 9. *Ailuropoda melanoleuca.* Lower jaw. × 1/3.
Fig. 10. *Thalarctos maritimus.* Lower jaw. × 1/3.

conule" and of very numerous small tubercles on the surface of the transversely widened talon. The development of a large talon on the posterior side of m^2 occurs independently in certain mustelids and in the last upper molars of the pigs. Hence the somewhat bear-like general appearance of the second upper molar of *Ailuropoda* is in itself not necessarily evidence of family relationship.

M^2 of *Ailuropoda* as compared with m^2 of *Arctotherium* lacks the sudden constriction in the outer wall behind the metacone (which constriction is characteristic of bears) and the surface of the transversely wide and massive talon is covered with many small but prominent tubercles, whereas in the m^2 of *Arctotherium* the tuberculation is sparse, minute and indefinite.

The second lower molar of *Ailuropoda* differs widely from those of all the bears and their allies in its much greater width, in the presence of high meta- and ento-conid transverse crests and in the presence of small polyisomerous cuspules on several parts of the crown.

The third lower molar of *Ailuropoda* is wider than that in typical bears and its crown is covered with many small tubercles.

Thus the cheek teeth of *Ailuropoda* differ widely from those of the bears in the following conspicuous features:

	Ailuropoda	Typical Bears
Upper p^2, p^3	Large and progressively complex	Very small and degenerate
Lower p_2, p_3	Large and progressively complex	Very small and degenerate
Upper carnassial (p^4)	Of large size with three large external cusps and very large postero-internal cusp	Of small size with two external cusps and no postero-internal cusp
Lower p_4	Large with trilobed blade flattened externally	Small, degenerate, crown with single tip
Lower carnassial (m_1)	Large, robust, with very large and distinct paraconid and metaconid	Much compressed, with weak paraconid and small metaconid
Upper m^1	Very large, squarish, with large "proto-" and "meta-"conules and massive internal cingulum	Smaller, elongate, without "proto-" and "meta-" conules, reduced internal cingulum
Upper m^2	Very massive, with broad talon, stout internal cingulum and many bead-like tubercles	Elongate, with narrow talon, slight internal cingulum and somewhat vermiculate surface

	Ailuropoda	Typical Bears
Lower m_2	Massive, broad, with high transverse meta- and entoconid crests and coarse tubercles. Trigonid and talonid subequal	Slender, compressed, with cingulum-like entoconid; trigonid and talonid asymmetric
Lower m_3	Large, short, wide, surface coarsely tuberculate	With oval surface, delicately sculptured

In general the hemicyons, as figured by Frick, in spite of retaining relatively large carnassials (an obviously dog-like and primitive character), definitely align themselves between the primitive dogs on the one hand and the bears on the other, and show no demonstrable tendency in the direction of *Ailuropoda* except a secondary widening of the molars in *Arctotherium*. In *Hyaenarctos* the large size of the carnassial, as compared with the molars, is a point of resemblance with the primitive dogs and miacids, while in *Indarctos* and *Ursavus* the increasing length of the molars points the way to the sharp degeneration of the premolars in the modernized bears.

The dentitions of *Arctotherium* and *Pararctotherium* closely connect themselves with those of the *Hyaenarctos-Indarctos* group and present only superficial resemblances to the dentition of *Ailuropoda* joined with many significant differences. Therefore, so far as the evidence of the dentition is concerned, we may look for the ancestry of *Ailuropoda* neither among the bears themselves nor among the near-ancestors and relatives of the bears, such as *Indarctos*, *Hyaenarctos* and *Arctotherium*.

Still greater are the differences that separate the dentition of *Ailuropoda* from those of the short-faced extinct dogs, such as *Borophagus* as figured by Matthew and Stirton (1930). Hence I can find in the foregoing comparative study of the dentition of *Ailuropoda* no support whatever for the conclusion of various authors who have classified it with the bears and particularly in the neighborhood of *Hyaenarctos*, nor even for the idea that *Ailuropoda* is any sort of intermediate between bears and procyonids.

COMPARISON OF THE CHEEK TEETH OF THE GIANT PANDA WITH THOSE OF *AILURUS* AND OTHER PROCYONIDS

It is perhaps not always realized even by palaeontologists that, in many families of vertebrates, structurally ancestral stages of any given horizon often persist to later periods and are the contemporaries of their more or less highly modified derivatives. This truth, which is of far-reaching and manifold significance, is nowhere better documented than

in the existing families of the fissipede Carnivora. Among the Procyonidae it was long since recognized by Wortman and Matthew (1899) that the existing genus *Bassariscus* has retained almost completely the ancestral canid characters of the upper and lower carnassials and molars, except that the metastyle shear of p^4 is reduced and that there is a small internal cingulum bearing a low postero-internal cusp. This is the first step toward the partial molarization of p^4, which is conspicuous in increasing degrees in *Nasua*, *Procyon* and *Ailurus*. In another direction *Bassariscus* is the structural ancestor of *Bassaricyon*, at least in its dentition, and the latter, with its rounded low-cusped p^4, m^1 and m^2, points the way to the flat-topped cheek teeth of *Cercoleptes* (*Potos*).

Likewise, *Bassariscus* may be regarded as the structural ancestor of *Procyon*, which, along with greatly increased size, has acquired more massive jaws; p^4 of *Procyon* has its metastyle blade greatly reduced, its "hypocone" (tetartocone) and main internal "protocone" (= deuterocone) much emphasized; its molars have enjoyed a marked increase in anteroposterior diameter, the main cusps having become large and rounded pyramidal. Similarly in its lower teeth, the carnassial (m_1) of *Procyon* has reduced its sectorial and increased its crushing features, while m_2 has become elongate and tubercular. *Nasua* is a long-snouted relative of *Procyon* with deceptively secondary equalization of the main molar cones. Its p^4, however, does supply a structural stage in the evolution of p^4 of *Ailurus*. *Ailurus* is much more advanced in its cheek teeth than any other existing procyonid but, as will be shown below, its cranial characters securely connect it with that family.

Turning to the fossil forms, *Phlaocyon* (Wortman and Matthew, 1899) is near the racoon but more primitive, while the related *Aletocyon*, as noted by Romer and Sutton (1927) shows several significant suggestions of *Ailurus* and tends to tie in that genus more securely with the Procyonidae.

Ailurus, in turn, is almost the direct structural ancestor of *Ailuropoda*, especially with regard to nearly all those features in which the latter contrasts widely with the bears. These comparisons may be conveniently summarized as follows:

	Ailurus	*Ailuropoda*
Upper p^2, p^3	Crowns large and progressively complex	Much larger and more elongate but with closely comparable cusps
Lower p_2, p_3	Large and progressively complex, compressed, tri-	Much larger and more elongate but with closely com-

	Ailurus	*Ailuropoda*
	cuspid, with shearing surface on outer side	parable cusps and similar shearing surfaces
Upper carnassial (p^4)	Of large size, with three large external cusps, two large internal cusps and an internal cingulum cusp	Much more elongate; postero-internal cusp greatly enlarged; internal cingulum cusp between two main internal cusps
Lower p_4	Elongate, outer face flattened and tending to become tricuspid	Strikingly similar in ground plan but with more advanced tricuspid arrangement of buccal cusps
Lower carnassial (m_1)	Large, robust, with very large conical paraconid and hypoconid; trigonid and talonid subequal	Much larger and with derived crown pattern
Upper m^1	Very large and wide, with four large main cusps; a parastyle, mesostyle and small metastyle; a large internal cingulum	Much larger, squarish, with reduced styles, large proto- and meta-conules and robust crenulate internal cingulum
Upper m^2	Smaller than m^1, but otherwise essentially similar	More elongate anteroposteriorly, with huge talon; crown with four main cusps and numerous secondary bead-like tubercles
Lower m_2	Elongate, narrow, with opposite proto- and metaconids; double metaconid and large hypoconulid	Widened, with subequal trigonid and talonid opposite proto- and metaconids, no hypoconulid and coarsely tuberculated crown
Lower m_3	Absent	Present, robust; shortened anteroposteriorly and irregularly tuberculated

Long experience with other anteroposteriorly elongate tuberculated molars in other families of mammals (especially in various herbivorous phyla) leads to the conviction that the striking and peculiar features of the second and third upper and lower premolars that are common to *Ailurus* and *Ailuropoda* far outweigh the conspicuous differences in the molars. These appear to be correlated with the highly specialized food habits of *Ailuropoda*, which cuts up bamboo leaves and stems and grinds them into small pieces. Even the presence of a third lower molar in *Ailuropoda* (Fig. 9) and its absence in *Ailurus* (Fig. 8) does not necessarily eliminate *Ailurus* from relatively close relationship to the direct

ancestors of *Ailuropoda*. The hypoconulid is lacking in m_2 of *Ailuropoda*, but the so-called third molar of this genus holds the same spatial relations to the internal alveolar ridge as does the hypoconulid of the second lower molar in *Ailurus*.

Two mutually exclusive hypotheses may be invoked to account for the presence of an m_3 in the, in general, more highly specialized genus *Ailuropoda* and its absence in the, in general, more primitive *Ailurus*.

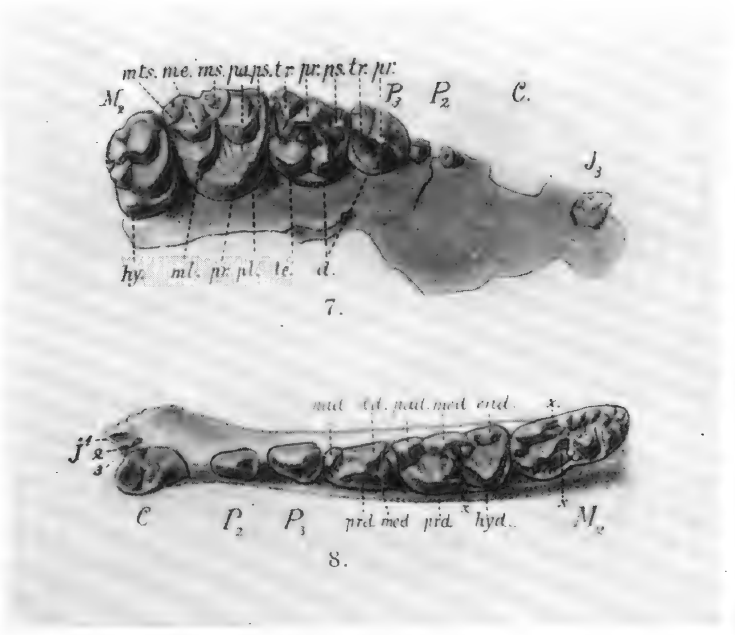

Fig. 11. *Parailurus anglicus*. Right upper and left lower teeth. × 1. After Schlosser.

The first, most obvious and easiest suggestion is that these two modern genera have descended along divergent paths from some ancient procyonid which had not yet lost the m_3 of primitive dogs and procyonids. The alternative hypothesis is that the great growth energy at the posterior end of the dental lamina has caused the splitting off of a new dental papilla, which would be as much a neomorph as are the occasional supernumerary posterior molars (m_4) of anthropoid apes and man. In its occlusal relations m_3 of *Ailuropoda* articulates behind the metacone of m^2 and directly with the great secondary talon of that tooth, while in *Ailurus* the hypoconulid of m_2 likewise articulates behind the meta-

cone of m^2. Thus it seems not unlikely that the so-called m_3 of *Ailuropoda* has appeared in adjustment to the enormous development of the talon of m^2. This hypothesis is not so far-fetched as it may seem to many palaeontologists, for it is fortified by the very numerous point to point agreements between *Ailurus* and *Ailuropoda* in many parts of the skull, as shown below. Moreover, A. E. and H. E. Wood (1933) have assembled cogent evidence for the view that in modern dogs a "third" upper molar does occasionally appear secondarily.

Unexpected support for the conclusion that the dentition of *Ailuropoda* is in general a structural derivative of that of *Ailurus* is supplied by the dentition of *Parailurus anglicus* as figured and described by Schlosser (1899). Here the upper "carnassial" (p^4) has become more elongate anteroposteriorly as compared with that of *Ailurus* and the entire crown pattern is distinctly approaching that of *Ailuropoda*. The unmistakably intermediate condition of the p^4 of *Parailurus* between those of *Ailurus* and *Ailuropoda* definitely disposes of Winge's suggestion (as stated by Bardenfleth) that the large postero-internal cusp of p^4 of *Ailuropoda* is not homologous with the corresponding cusp of *Ailurus*.

The first and second upper molars of *Parailurus*, although somewhat more elongate than those of *Ailurus*, do not yet show the breaking-up of the surface of the crown into secondary polyisomeres. The lower "carnassial" (m_1) is fairly suggestive of that of *Ailuropoda*. M_2 is large and progressive, with a small hypoconulid, which articulated with the posterior part of m^2, as does the hypoconulid of m_2 of *Ailurus*.

In conclusion, although the molars of *Ailuropoda* differ from those of *Ailurus* in superficial appearance, to such an extent indeed that Winge and Bardenfleth would not allow any close relationship between these genera, yet the differences between them, especially the greater complexity of the upper molar crowns in *Ailuropoda* and their anteroposterior elongation, are somewhat similar to the differences between the multituberculate upper molars of progressive Suidae and the quadrituberculate molars of their bunodont ancestors. In other words, such differences seem to be correlated with differences in food habits.

COMPARISON OF THE MANDIBLE AND SKULL OF *AILUROPODA* WITH THOSE OF OTHER ARCTOID CARNIVORA

When we arrange the skulls of various arctoid carnivores in side view on the Frankfort plane, we see that in *Ailurus* (Fig. 1) the tooth row is curved somewhat upward; in *Ailuropoda* (Fig. 2) it is nearly horizontal,

while in the bears it is inclined downward. Typical dogs have the temporo-mandibular articulation only a little above the general level of the occlusal plane, whereas in *Ailurus* this articulation is well elevated above the occlusal plane. As a consequence of the backward extension of its molars and the huge size of its temporal fossa, the coronoid process is of great vertical extent, its anterior border forms a forwardly inclined sigmoid curve and its masseteric fossa is exceptionally deep and constricted. In *Ailuropoda* (Fig. 6), in which the tooth rows have become more than twice as long anteroposteriorly as they are in *Ailurus* (Fig. 5), the temporo-mandibular articulation has been displaced to the rear, the extreme constriction of the masseteric fossa (Fig. 2) has been rectified and the sigmoid curvature of the anterior border of the coronoid process reduced. The backward displacement of the glenoid socket of the squamosal in *Ailuropoda* has likewise decreased the excessive upbowing of the zygomatic arch, which is so conspicuous in *Ailurus* (Fig. 1); but in all these parts *Ailuropoda* differs widely from the bears (Figs. 3, 7) and its conditions are most readily derivable from those seen in *Ailurus*. A conspicuous difference between *Ailuropoda* and *Ailurus* is found in the extreme heaviness and density of the jaw bones of the former; but this is evidently due to some obscure physiological difference involving calcium metabolism and the endocrine glands.

In *Ailurus* (Fig. 1) the hook-like angle of the mandible is on a plane far above that of the lower border of the mandible. The same is true in *Ailuropoda* (Fig. 2), but here the posterior displacement of the articular facet (glenoid) has further emphasized the reduction of the angle. In the bears (Fig. 3) both the condyle and the angle are on a lower plane and the angle is not reduced. The postglenoid process of the squamosal in *Ailurus* (Figs. 1, 5) extends far downward and forward below the level of the outer part of the mandibular condyle, so as to articulate with a downward prolongation of the inner part of that condyle. The result is a peculiar scroll-like temporo-mandibular articulation which is most nearly paralleled in the Mustelidae. In *Ailuropoda* (Figs. 2, 6) the conditions in this region are directly derivable from those in *Ailurus*, with the addition that the backward displacement of the glenoid articulation has caused the postglenoid process to overlap and fuse with the inferior surface of the tympanic bulla. The bulla of *Ailuropoda* (Fig. 6) differs from that (Fig. 5) of *Ailurus* (which is inflated) by being small and deflated, as it is in many large mammals as compared with their smaller relatives.

In general the masticatory part of the skull of *Ailuropoda* is wholly

unlike the bears and almost immediately derivable from that of *Ailurus*, the leading factors being the great increase in absolute size of the entire animal, the relative increase in the backward extension of the molars and their further evolution away from the simple quadrituberculate toward a coarse, mill-like type covered with small tubercles. It is therefore not surprising to learn from Mr. Carter that the food of *Ailuropoda* consists chiefly of leaves and stems of bamboo. Thus *Ailuropoda*, although a carnivore by ordinal heritage, is assuming the masticatory habitus of a herbivore, whereas its structural ancestor *Ailurus* has retained a more omnivorous habitus.

We may therefore sum up this part of our analysis in the following table:

	Ailurus	*Ailuropoda*	Bears
Muzzle	Short	Very short	Usually long
Bony forehead	Of moderate width	Very narrow	Very broad
Maxilla in side view	Inclined slightly upward	Inclined slightly upward	Inclined downward
Zygomatic arches	Sharply bowed outward and downward	Less sharply bowed outward and downward	Elongated
Alveolar pouches of maxillae	Conspicuous in top view of skull (Fig. 12)	Very conspicuous in top view (Fig. 13)	Not seen in top view (Fig. 14)
Sagittal crest	Moderate	Very high, elongate posteriorly	Relatively low
Lower border of mandible	Strongly convex	Convex	Flat
Level of condyle	Far above plane of cheek teeth	Above cheek teeth	On or below level of cheek teeth
Angle of mandible	Slightly inflected	Strongly inflected	Not inflected
Coronoid process	Very high with strongly convex anterior border inclined forward, tip produced backward	High, convex anterior border, tip produced sharply backward	Low and broad with sloping anterior border
Mandibular condyle	Scroll-like, much extended postero-medially	Scroll-like, with large postero-medial extension	Transverse cylindrical, with but little if any postero-medial extension
Postglenoid process of squamosal	High, internally placed	High, internally placed (relatively near to midline) and far to the rear	Low, far out from midline and displaced forward

	Ailurus	*Ailuropoda*	Bears
Posterior base of postglenoid process	Not overlapping tympanic bone	Strongly overlapping tympanic bone and fused with it	Sharply separated from tympanic bone
Mastoid process	Small, rounded, directed outward	Very large, projecting outward, downward and forward below tympanic	Short, thick
Paroccipital process	Longer than mastoid process	Much shorter than mastoid process	Short

Lankester (1901), correctly as it seems to me, recognized and interpreted the striking agreements in the mandible between *Ailurus* and *Ailuropoda* and the wide differences of the latter from the bears in this region. Bardenfleth, on the other hand, attributed the fundamental resemblances between *Ailurus* and *Ailuropoda* to convergence but accepted the general resemblances between the upper molars of *Ailuropoda* and those of the Ursidae as indicative of family relationship.

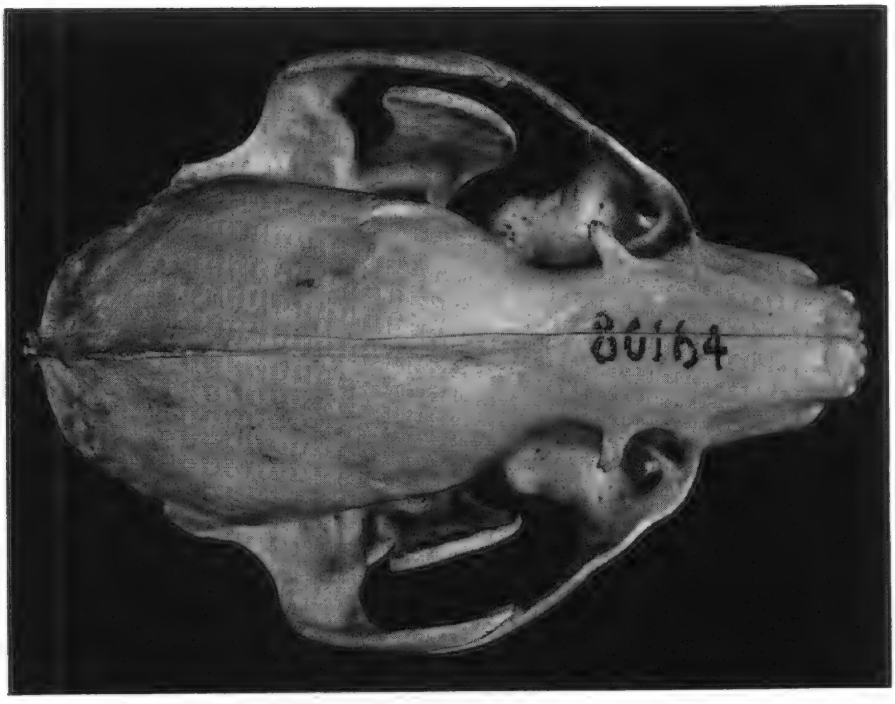

Fig. 12. *Ailurus fulgens.* Upper side of skull. × 1.

Passing to a comparison of those parts of the skull which are more closely related to the brain and cranial nerves, we find that in *Ailurus* what may be called the optic funnel (Fig. 1) leading back from the orbit

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Fig. 13. *Ailuropoda melanoleuca.* Upper side of skull. × 1/3.
Fig. 14. *Thalarctos maritimus.* Upper side of skull. × 1/3.

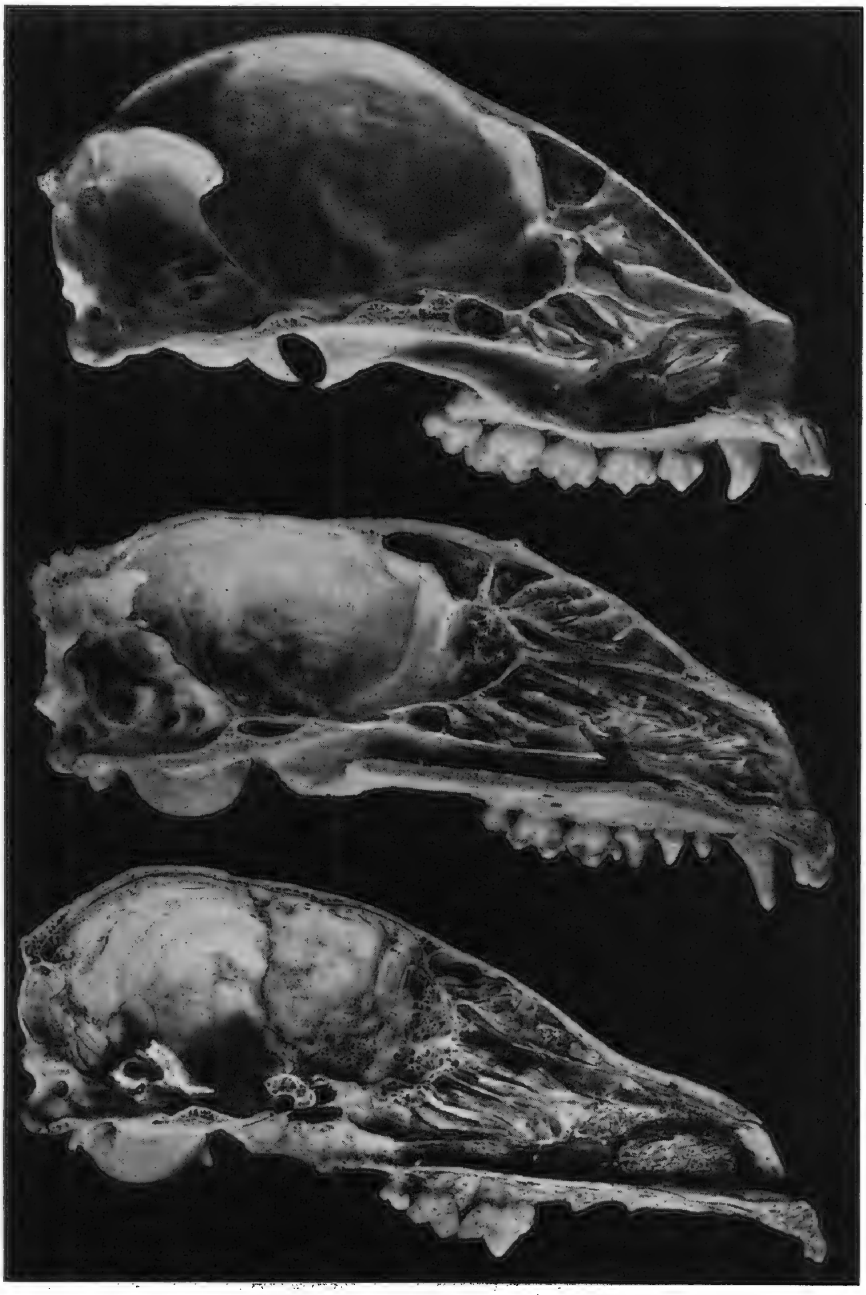

Fig. 15. *Alopex* sp. Left half of skull, mesial aspect. Not to scale.
Fig. 16. *Procyon*. Left half of skull, mesial aspect. Not to scale.
Fig. 17. *Ailurus*. Left half of skull, mesial aspect.

to the optic foramen is bounded by a faint oblique ridge which culminates above in the delicate postorbital process. In *Ailuropoda* (Fig. 2) little if any trace of this ridge is visible; in the bears (Fig. 3), including *Arcto-*

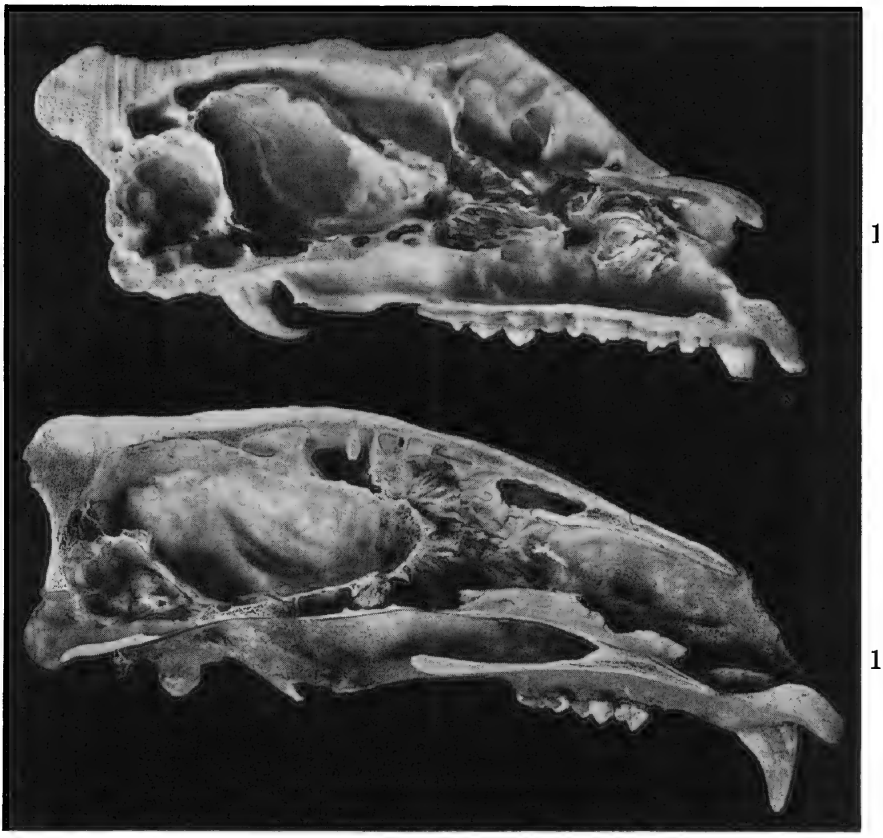

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Fig. 18. *Ailuropoda.* Left half of braincase, mesial aspect.
Fig. 19. *Thalarctos.* Left half of braincase, mesial aspect.

therium, on the contrary, this ridge is greatly emphasized and is continued backward and downward laterally to the foramen lacerum anterius.

Longitudinal bisection of the cranium of a series of representative arctoids yields further evidence that *Ailuropoda* is more closely related to *Ailurus* and the Procyonidae than to the bears. Figures 15 to 19

indicate that in the fox and polar bear the tentorial plane is sharply directed backward and the chamber for the cerebellum is relatively small. However, this condition is much more pronounced in the polar bear (*Thalarctos maritimus*) (Fig. 7) than it is in the black bear (*Euarctos americanus*). *Ailuropoda* (Fig. 9) is much more specialized than the bears in the extreme shortness of the base of the occiput, the distance from the basion to the posterior clinoid process being about fifteen per cent of the basal length (basion to prosthion), whereas in both *Euarctos americanus* and *Ailurus* it is about twenty-four per cent.

Another mark of specialization in *Ailuropoda* is the virtual disappearance of the fossa subarcuata, which remains widely open on the dorsum of the petrous bone in fox, *Ailurus*, and bears but is indistinct in an aged *Procyon*.

In *Ailuropoda* (Fig. 13) the medial part of the tentorium is more nearly vertical and the cerebellar chamber is more expanded dorsally. In *Ailurus* also (Fig. 12) the tentorium and cerebellar cavity are expanded dorsally more than in *Procyon* (Fig. 16) and much more than in the fox (Fig. 15). The cavity of the cerebrum in *Ailuropoda* is relatively short, high posteriorly and sharply sloping anteriorly, while that in the bears (Fig. 14) is relatively longer with less depressed frontal wall. In *Ailurus* the frontal pole of the brain is expanded dorso-anteriorly, as it is also in *Procyon* and the fox; but in these animals the frontal sinus is of moderate size, whereas in *Ailuropoda* it has grown far backward above the cerebellum, extending also vertically but limited laterally by the powerful anterior fasciculi of the temporal muscle, so that externally the forehead is extremely narrow. In the bears, on the contrary, the frontal sinuses expand laterally, producing the characteristically broad forehead. The olfactory fossa in *Ailuropoda* is relatively very small, whereas in bears it is larger. In *Ailurus* the olfactory fossa is relatively larger than in *Ailuropoda*, more as in *Procyon*, but not nearly so large as in the fox.

In *Ailuropoda* the large maxillo-turbinate scrolls do not seem to present any striking differences from those of either the bears or *Ailurus*, which all alike conform to the "arctoid" plan. The nasal chamber as a whole is shorter and higher in *Ailuropoda* and *Ailurus* than in the bears.

In *Ailuropoda* the internal opening of the spheno-palatine foramen is somewhat fissure-like and faces forward. In the bears it is a very large oval window, which looks more directly inward. In *Ailurus* the conditions foreshadow those in *Ailuropoda*.

Table I.—Comparative skull measurements (in millimeters)

	Ailurus	*Ailuropoda* 1	" 2	" 3	" 4	*Paraarctotherium*	*Tremarctos ornatus*	*Helarctos malayanus*	*Euarctos americanus*	*Ursus maritimus*
		Three Females			Male					
(1) Skull, length (pmx-cond.) (L)	95	255	247	247		325	194	197	286	307
			av. 249		258					
(2) Transverse zygomata (B)	71	208	196	204		218	115	139	183	172
			av. 202		214					
I. Index $\frac{B \times 100}{L}$	74.7		85		83	67	59	70	64	56
(3) Width of forehead (in front of postorb. proc.) (wf)	20	55	52	49	54	101	48	53	76	75
			av. 52							
II. Index $\frac{wf \times 100}{L}$	22		20.9		20.9	31	24.7	27	26	24.4
III. Index $\frac{wf \times 100}{B}$	28		25.7		25.2	46	41.5	39	41.5	43.6
(4) Length, midpoint (between postglenoid proc.) to basion 1 (pgl)	19	40	37	38		60	43	49	71	72
			av. 38		39					
IV. Index $\frac{l(pgl) \times 100}{L}$	20		15		15	18	22	25	24	23
(5) Length mandible, cond. to inc. (lmd)	72		200			...	137	132	196	206
(6) Height, tip coronoid to bottom of mandible below angle (hmd)	39	115	116	120		...	63	63	98	80
			av. 117		118					
V. Index $\frac{(hmd) \times 100}{(lmd)}$	54		58			...	43	47	50	39
(7) Height of head when resting on fore part of mandible (H)	66	204	208	200		...	110	105	143	121
			av. 204		216					
VI. Index $\frac{H \times 100}{L}$	69		81		84	...	56	53	50	39

N. B.—It will be seen that in nearly all its proportions the skull of *Ailuropoda* is nearer to that of *Ailurus* than to those of any of the bears.

Doubtless the analysis could be carried into additional details but enough has been said to indicate that the architecture of the inner aspect of the brain case of *Ailuropoda* is not inconsistent with the con-

clusion that this genus is simply a specialized member of the subfamily Ailurinae, and that the bear-like character of the maxillo-turbinate scrolls is shared with *Ailurus* and *Procyon*.

Some palaeontologists will no doubt prefer to treat the Ailurinae (including *Ailuropoda*) as a separate family. In that case we should have to split the Procyonidae into the Bassariscidae, Cercoleptidae, Procyonidae (*sensu strictu*) and Ailuridae, but this would only disguise the fact that *Ailurus* in the deeper characters of its brain case is related to *Procyon* rather than to any known canids or ursids.

My conclusions are briefly as follows: (1) that Lankester and Lydekker were right in referring *Ailuropoda* to the subfamily Ailurinae of the Procyonidae; (2) that such resemblances as it shows to the bears in the dentition are due largely to convergence; (3) that *Ailurus* is a specialized procyonid; (4) that all the bears (including *Hyaenarctos*) have been derived from a branch of the primitive canids which was quite distinct from that which gave rise to the procyonids, including *Ailuropoda*.

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APPENDIX

Through the great kindness of Dr. Gerrit S. Miller of the United States National Museum, I have had the privilege of studying a young skull determined as *Ailuropus melanoleucus*, from Szechuan (U. S. Nat. Mus. No. 259076), in which the cranial sutures are for the most part wholly open. All the permanent cheek teeth are in place but only the earliest beginnings of wearing facets are seen on the cutting edges of the teeth.

The numerous points of special resemblance to *Ailurus* noted in the

Fig. 20. *Ailuropoda melanoleuca*. Young adult skull, showing sutures. Side view.
U. S. Nat. Mus. No. 259076.

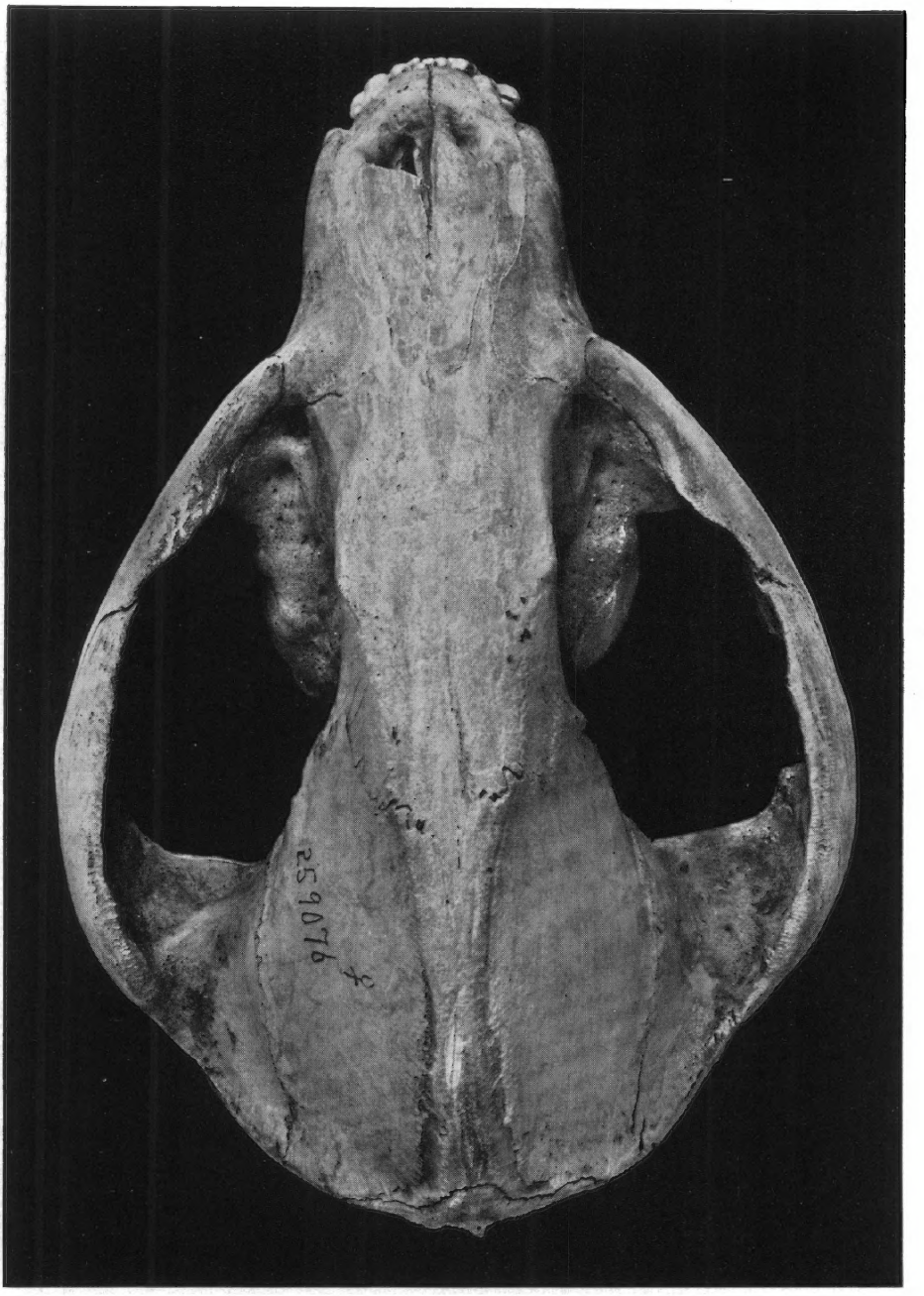

Fig. 21. *Ailuropoda melanoleuca.* Young adult skull, showing sutures. Top view. U. S. Nat. Mus. No. 259076.

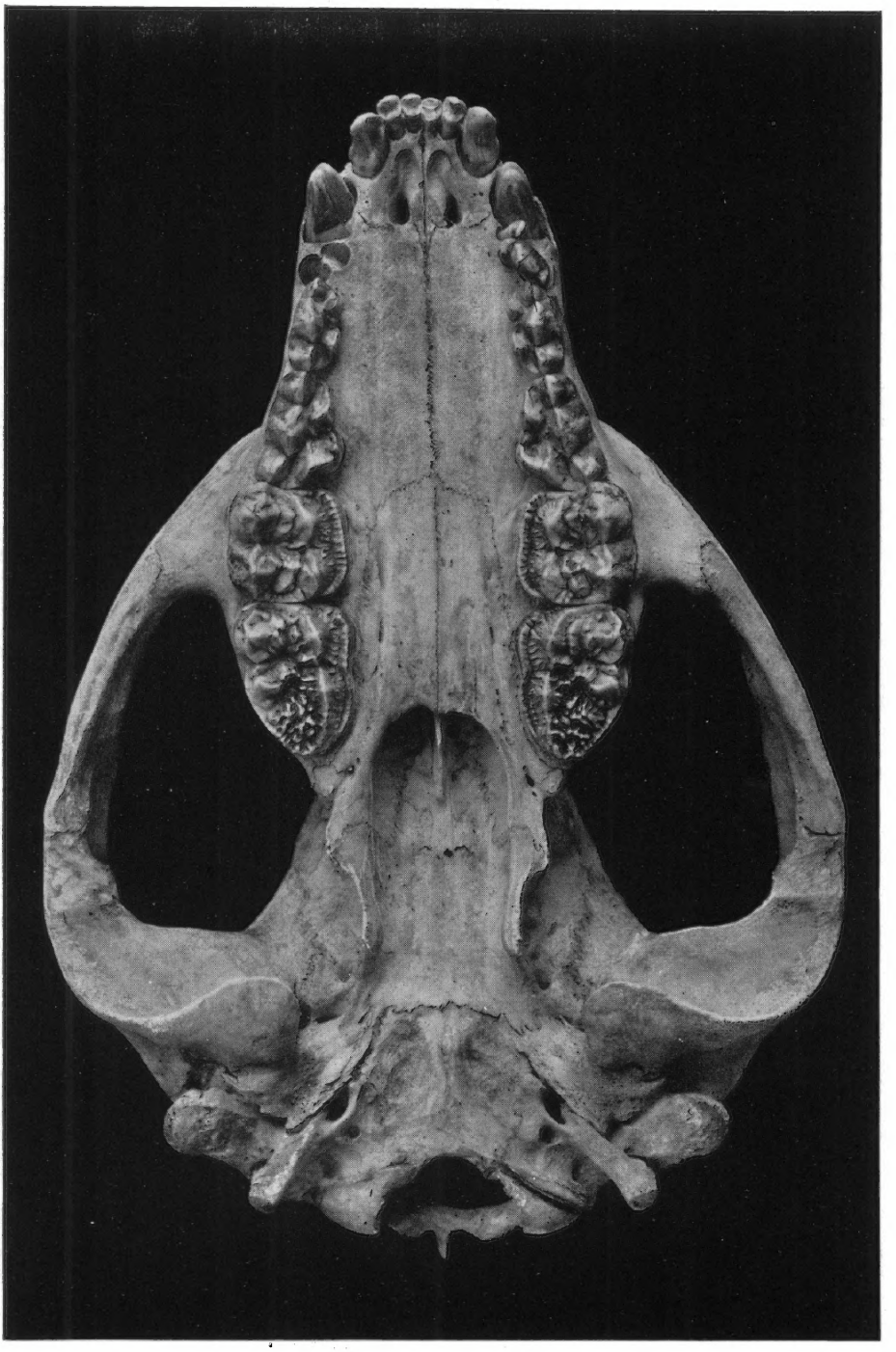

Fig. 22. *Ailuropoda melanoleuca.* Young adult skull, showing sutures. Under side. U. S. Nat. Mus. No. 259076.

foregoing paper are all sustained and emphasized by the conditions in the young skull. Sharp contrast with the bears is seen in the region immediately behind the floor of the orbit, where the great maxillary alveolar pouches, already conspicuous in *Ailurus*, have now grown medially, nearly closing the fissure between themselves and the vertical plate of the palatine and forming with the latter a secondary contact posteriorly.

In the bears, on the contrary, the alveolar portions of the maxilla are very narrow transversely, but little produced behind the floor of the orbit and do not form a *secondary* contact with the posterior part of the palate. In the occipital region the young skull of Ailuropoda offers many resemblances to that of *Ailurus*, especially in its great width and lowness, in the form and direction of the paroccipital process and in the shortness of the mastoid process, which extends downward, outward and forward to a much less degree than in the old skulls. The fusion of the postglenoid with the tympanic has barely begun and the spout of the tympanic, although reduced, is still recognizable.

There is no median anterior palatine foramen either in *Ailuropoda* or *Ailurus*, whereas in the bears (including *Arctotherium*) this median foramen is conspicuous. The chief cranial foramina compare closely with those of *Ailurus*.

The lacrymal, however, is greatly reduced in size and confined within the orbital rim, as in both *Ailurus* and the bears.[1] In both *Ailurus* and *Ailuropoda* the lacrymal is separated from the orbital wall of the palatine by the alveolar extension of the maxilla. At least in some bears the primitive lacrymal-palatine contact is retained; in others (e.g., *Helarctos*) the palatine seems to be excluded from contact with the lacrymal by the maxilla. In both *Ailuropoda* and the bears the lacrymal foramen is double.

[1] See also Gregory, William K., 1920. 'Studies in comparative myology and osteology, No. IV.—A review of the evolution of the lacrymal bone of vertebrates with special reference to that of mammals.' Bull. Am. Mus. Nat. Hist., XLII, Art. 11, 95–263.